STUDIES ON THE LIFE HISTORY OF THE MARINE ANNELID *NEREIS VEXILLOSA*

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Introduction

Nereis vexillosa Grube is the most abundant member of the larger annelids of the Pacific northwest fauna. In Puget Sound it attains a size of about 30 cm. but, as will be explained later, some heteronereid individuals may be only about 6 cm. long.

It is characteristically a cold water form occurring intertidally and in shallow water from eastern Siberia, Alaska and southward along the northwest American coast to Santa Barbara, California. Some reports extend its range as far south as San Diego. In the southern range, however, it may have been confused with *Nereis mediator* Chamberlain (Chamberlain, 1919) or with *Neanthes succinea* (Frey and Leuckart) according to Hartman (personal communication). The apparent absence of the specific egg masses, described below, from the southern range lends support to the belief that *N. vexillosa* may not occur in these waters.

The tiny eggs produced by this animal are about 0.2 mm. in diameter; they are spawned in firm, irregular gelatinoid masses, somewhat translucent, and of blue-green, greenish or brownish tints (Figure 1). These colors are most noticeable in the freshly laid eggs owing to their greater compactness prior to absorption of water by the capsular material. The firmness of the masses enables them to withstand a good deal of handling or washing about on the beach by waves without disintegrating. Hence they are often found in good condition on tidal flats where bits of seaweed or other debris collects at the waters edge. They appear never to be found in more than moderate quantities despite the abundance of the species producing them.

In so far as known, there is no other nereid worm that deposits its eggs in this manner. Commonly the eggs of other species of the genus, or of closely related genera are deposited separately in the water or are only lightly agglutinated. The size of masses varies considerably being about one to three inches in diameter, apparently depending upon the size of the female depositing them.

The identity of the egg masses has long been a puzzle to biologists and others alike, and, indeed, the present study was initiated in 1927 at Friday Harbor, Washington, primarily for the purpose of identification. In the course of the investigation, however, important aspects pertaining to the life history of the species have come to light.

It is a pleasure to acknowledge the generous support given this investigation by Director T. G. Thompson, Professor T. Kincaid, and other members of the staff of the University of Washington Oceanographic Laboratories where facilities

were provided for much of the work. My thanks are also due to Dr. Olga Hartman of the Allen Hancock Foundation for identification of the heteronereis worm and for helpful suggestions.

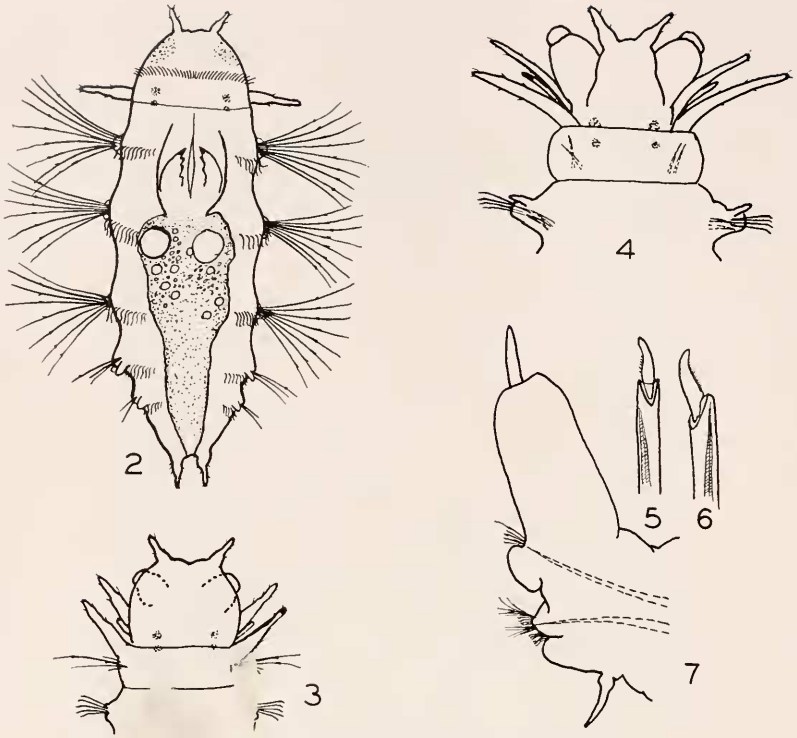
FIGURE 1. *Nereis vexillosa*. A small egg mass, about natural size.

CULTURE EXPERIMENTS AND DEVELOPMENT

The larvae resulting from culture of eggs collected in 1927 failed to survive long beyond hatching and therefore served to establish only that they were annelids of the nereid type. The failure of these to survive may be due in part to inadequate food since they were fed only diatoms and algae. This diet brought good results with *Platynereis agasszi* which was being reared at the same time (see Guberlet, 1933), but subsequent experiments have indicated that *Nereis vexillosa* thrives best in later life when animal food is provided.

In the summer of 1941 an opportunity was again presented to set up cultures at Friday Harbor. Two egg masses were found in False Bay and rearing of the larvae began on June 28. Some of the larvae were already hatching in the three to five segmented stage (Figure 2). The larvae and young worms grew slowly and were able to survive for about a week after hatching on the yolk content which became concentrated in the digestive tract. Later they were fed sessile diatoms (*Navicula sp.* and *Biddulphia laevis*) and powdered dry scallop muscle.

The rate of growth varied so greatly that on August 23 the most advanced worms, now about 57 days old, had acquired 35 segments and were about 9 mm. long, whereas the least advanced had but 15 segments and were about 5 mm. long.



FIGURES 2–7. *Nereis vexillosa.*

FIGURE 2. Five-segmented larva.
FIGURE 3. Head of eight-segmented larva to show development of peristomial tentacles.
FIGURE 4. Head of fifteen-segmented larva to show further progress of head development.
FIGURES 5 and 6. Homogomph notoseta and heterogomph neuroseta from parapodium shown in Figure 7.
FIGURE 7. Parapodium from posterior portion of body of eleven month old worm.
(Camera lucida drawings, Figures 2, 3, 4 same scale; Figures 5, 6, 7 enlarged scale.)

It was however, still not possible to establish identity of the worms from the most advanced specimens, therefore, at the end of the summer session the animals were moved alive to the Scripps Institution of Oceanography at La Jolla, California. This was accomplished by placing ten specimens of various sizes in each of four vials with sea water and containing a wad of cotton among the strands of which the young worms found protection against violent battering in the vials while in transit. The vials were kept cool by being wrapped in wet, frequently-changed paper towels.

Upon arrival at La Jolla the specimens were changed gradually to local sea water (salinity about 3‰ above that at Friday Harbor) in small culture dishes and it was found that 25 had survived the journey. Following some additional mortality in the first month, 16 of various sizes lived for several months.

After setting up the cultures at La Jolla, about three-fourths of the water was changed in each dish every two or three days and the animals were fed dried

powdered pecten and sea mussel for a few weeks, but growth was so slow that it was decided to try feeding finely chopped pieces of freshly killed *Thoracophelia mucronata*, a polychaete worm found abundantly at La Jolla. This fresh food was given in small quantities every second or third day. With it there was a prompt response by more rapid growth. Later bits of fresh mussel were also fed but the minced worms seemed to be preferred. Not only the killed and minced worms were eaten but living specimens half the size of the young Nereis were eaten. This rapacious habit was evident even in worms only 6 or 8 mm. long that were seen to grasp and completely swallow in a few seconds others of their kind that were fully half their own size. Diatoms were also added to the dishes and these were readily eaten. The animals rejected partially decomposed food and since the object of the experiment was to keep them growing as long as possible no further experimenting with food was deemed advisable. Results indicate that *N. vexillosa* is more or less omnivorous, utilizing mostly animal food but that it is not a scavenger by preference. According to Copeland and Wieman (1924) *Nereis virens* is also omnivorous though Gross (1921) found only evidence of plant feeding.

No membranous tubes were constructed as in *Platynereis agasszi*, only flimsy tubes of sand and debris were formed with the aid of secreted mucus, and after the animals had reached a length of about 15 mm. they rarely left their tubes completely to gather food. To facilitate study, pieces of glass tubing were provided and these were readily accepted in most cases. Some animals refused to accept new glass tubes that were provided to replace those outgrown and deserted. In these instances the lack of security resulted in restlessness and failure to feed normally.

The older specimens were kept in running (uncooled) sea water pumped in from the sea. At the middle of July this water had reached a temperature of 20° C., which is about 6 to 8 degrees higher than might be expected in the natural habits of *N. vexillosa* near Friday Harbor during the summer. This may well have been a contributing factor in the failure of the worms to survive with the advance of summer at La Jolla.

In Table I is given a summary of the condition of the worms that survived ten or more months. Two of these were found dead (May 18 and May 29). The others were killed and preserved only after they had deserted their tubes and it seemed obvious that they would not survive much longer.

At the age of four and one-half months, when about 60 segments had been formed, the worms reared from the 1941 egg masses had developed specific characteristics of *N. vexillosa*. Especially characteristic are the elongate strap-like dorsal ligules (Figure 7) of the parapodia of the posterior region of the body, but the head structures and the setae of the posterior region are also distinctive (Figures 5 and 6) in older specimens.

The process of cephalization is shown in Figures 2, 3, and 4. In this development, the first setigerous segment of the early larva becomes modified to form the peristomium. The anterior dorsal pair of peristomial tentacles appear first, followed by the posterior dorsal pair which develop from the first larval parapodium. A ventral pair of anterior peristomial tentacles then appear and finally the posterior ventral pair of tentacles are in evidence when the worm has acquired about 18 to 20 segments.

TABLE I

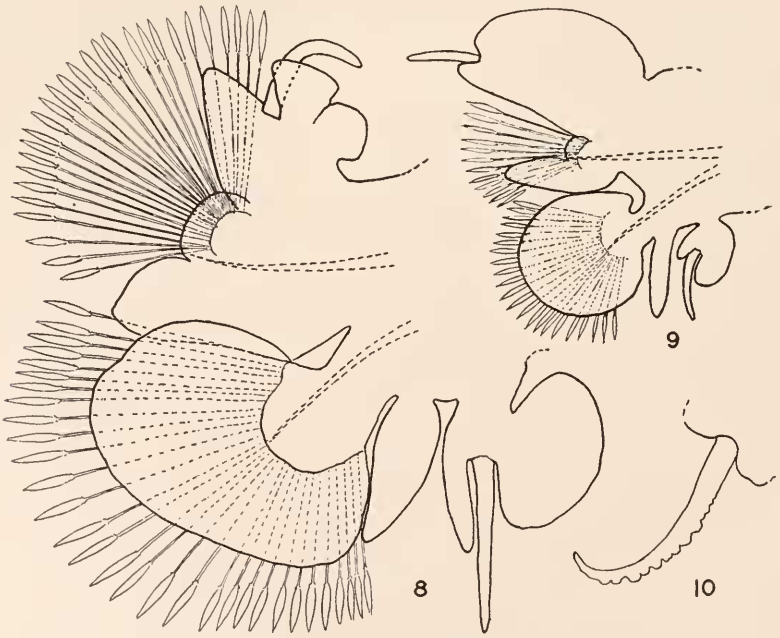
Nereis vexillosa. The seven oldest specimens from cultures set up at Friday Harbor, June 28, 1941

Date killed or found dead 1942	Number of segments	Approximate length when moderately relaxed
April 25	128	8 cm.
May 18	109	5 cm.
May 26	109	6.7 cm.
May 26	107	4.5 cm.
May 29	119	8.5 cm.
June 10	105	7 cm.
July 28	125	10 cm.

None of the specimens showed any indication of entering the heteronereis phase. In this respect they differ from *Platynereis agasszi*, several of which were found to enter this phase near the end of the first year.

SPAWNING HABITS

While culturing the larvae at Friday Harbor in 1941 a watch was kept for spawning adults in the bay. Finally from isolated small, spawning heteronereids there was obtained several masses of eggs. These spawners proved to be *Nereis*



FIGURES 8–10. *Nereis vexillosa.*

FIGURE 8. Heteronereized female parapodium, middle portion of posterior body.
FIGURE 9. Heteronereized female parapodium, fourth from last segment.
FIGURE 10. Dorsal cirrus, heteronereized male parapodium.
(Figures 8, 9, 10 camera lucida drawings to same scale.)

vexillosa Grube thus confirming the identification of the worms reared experimentally from egg masses collected in the field. Heteronereized parapodia are shown in Figures 8 and 9. Heteronereis males have 25 parapodial segments in the anterior portion of the body while the females have 27 such segments (count of 12 males and four females). In the males the dorsal cirrus of the heteronereized segments bears a series of wart-like protuberances on the ventral surface (Figure 10) while in the females examined these cirri were smooth.

The spawning worms were obtained only at night while collecting with a light at the end of the pier in front of the laboratories. They appeared only in small numbers usually an hour or two before midnight and were mingled with spawning swarms of the smaller species *Platynereis* (formerly *Nereis*) *agasszi* which on all occasions was the first of the two to appear swimming at the surface. It was not possible with these few observations to establish any correlation of spawning with phases of the tide or moon as has been done with other marine worms (cf. Woodworth, 1907; Lillie and Just, 1913; Guberlet, 1933).

Only small individuals of *N. vexillosa* were seen spawning and from what has subsequently been learned through the above rearing experiments, it seems certain that these were all spawning for the first time at the age of one year. Not only were some of the experimentally reared worms as large at the age of 10 to 11 months as some of the spawning worms but there was also indication of approach to sexual maturity. One of the worms reared at La Jolla was killed April 25, 1942 after having deserted its tube. Upon examination it was found to contain many eggs which were very small and not yet ripe, but their large numbers might be interpreted to indicate that spawning would normally have occurred in the coming summer. A second worm that died May 29 also showed many eggs. However, it seems certain that in nature some heteronereis individuals must be older than one year at spawning since egg masses of much greater size than those known to have been spawned by the smaller specimens have been found. This is more fully discussed later.

In nature more males than females were observed swimming at the surface. They are the first to come to the nuptial party where, as scattered individuals, they suddenly appear from below and rise to the immediate surface, swimming a few moments there in spirals and loops and then disappearing into the deeper water or the darkness beyond the range of the collector's light. They continue unabated in numbers and vigor as the females a little later appear to join the dance, a dance which seemingly is a climax that marks the ends of their lives, for none of the exhausted individuals kept in captivity was observed to live more than a few days following the act of spawning.

Isolated small heteronereis females ripe with eggs were induced to spawn almost instantly when a few drops of sperm laden water were added to the water in which they were isolated. This is similar to the findings of Lillie and Just (1913) for *Nereis limbata* and of Just (1929) for *Platynereis dumerilii*. In large battery jars the act of spawning by the female *Nereis vexillosa* consists of coming to or near the surface and suddenly exuding a mass of eggs which instantly agglutinates (Figure 11). She then passively sinks to the bottom together with the mass. A few moments later she frees herself from the mass which remains demersal and which in a few hours swells to about three or four times its original size through the absorption of water. The spawning of these demersal masses

in water just beyond the low tide limit may account for the finding of fewer egg masses than are commensurate with the number of worms.

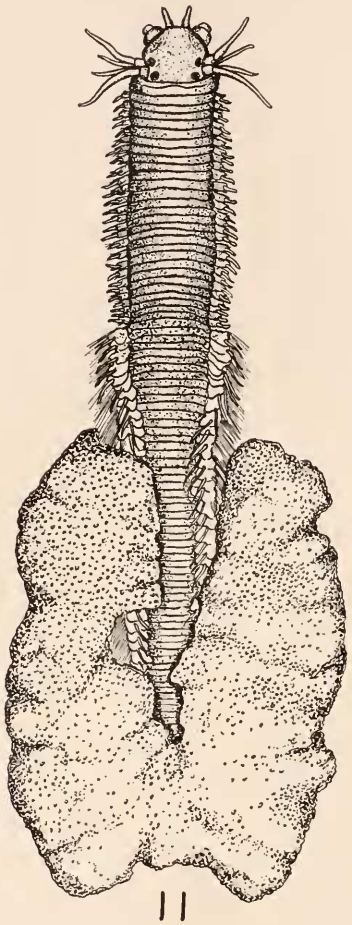


FIGURE 11. *Nereis vexillosa.* Method of egg deposition by small heteronereis. (Free hand drawing.)

DISCUSSION

An answer has been found as to the identity of the egg masses, and certain features of the life history of the species have been discerned. In the process of interpreting the observations, however, another biologically important question arises, namely, does *Nereis vexillosa* possess a diversified life history in which there may be recognized several types of reproductive individuals, as indicated for *Platynereis dumerilii* by Hempelmann? In the latter species at Naples, Hempelmann (1911) distinguished (1) small sexually mature nereis (i.e., atokus) individuals that gave rise to heavily yolked eggs producing characteristic larvae which he called "nereidogene"; (2) small heteronereis forms producing less

heavily yolked eggs developing into pelagic larvae called "planktogene"; (3) large heteronereis forms with eggs as in the small form but whose larvae have not been investigated. He found that after spawning, the small nereis form may in experimental cultures be transformed into a small heteronereis form and produce young for the second time and is therefore dissogenous. The nereis form may also grow to a relatively large size and then transform to the large heteronereis but the steps involved in arrival at the large form in this phase are uncertain. It is believed that entrance into the heteronereis form and its spawning marks the end of life for the individual.

More recently Just (1929) also worked on the Naples species and in so far as his investigation was carried, the findings of Hempelmann were verified.

It has been noted by H. P. Johnson (1901) that the heteronereis form of *Nereis vexillosa* occurs in individuals of 56 mm. and upward in length but the maximum length is not given. The same author reports that sexual maturity is frequently arrived at by the species without it becoming heteronereized. Ricketts and Calvin (1939) report finding many large heteronereis of *N. vexillosa* but the authors never found these to be free-swimming. The supposition is, however, that they do spawn, and indeed the finding of egg masses in Puget Sound that are much larger than those known to have been spawned by small heteronereis forms of the species substantiates this.

What the destiny of the worms reared from the Friday Harbor material would have been normally can be only a matter of conjecture. In this connection it may be significant to note that the number of segments in several large (14 to 21 cm. long) *N. vexillosa* collected in the field at Friday Harbor was 142 to 152 in the nereis phase, whereas the spawning heteronereids taken in the same region had only 63 to 96 segments. The latter figure is less than the number occurring in the seven most advanced specimens reared in cultures (Table I). These specimens had 107 to 128 segments and the length of some was greater than the spawning worms. This may mean that the reared worms were destined to reach sexual maturity only in a more advanced nereis phase or in a large heteronereis phase. Much additional study is needed to answer this question. The great range in size that is possible in the heteronereis of *N. vexillosa* should make it an ideal species for such a study if culture problems can be overcome.

Summary

Nereis vexillosa deposits its eggs in firm irregular gelatinoid masses which vary in size from about one to three inches in diameter.

Spawning of small (6 to 8 cm. long) heteronereids of this species was observed to take place an hour or two before midnight. The eggs which are demersal are apparently spawned in water at or just beyond the extreme low tide level and this habit may account for the finding of fewer egg masses than seems commensurate with the number of the species producing them. Isolated heteronereis females were induced to discharge their eggs by the introduction of spermatozoa into the water.

Worms cultured in the laboratory from egg masses collected on the beach throve best on fresh animal food. A number of young worms transported from Friday Harbor to La Jolla attained a maximum length of 10 cm. at the age of 13 months after hatching. All had acquired specific characteristics but none

became heteronereized. The transformations taking place during cephalization are similar to that occurring in other nereid worms.

Since the above maximum size of the reared worms is comparable to that of the small spawning heteronereis forms, it appears that the latter were spawning at the age of about one year. Much larger nereis and also heteronereis individuals are known to occur in this species but the time and steps involved in their development are unknown.

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